TICODENDRON PALAIOS SP. NOV. (TICODENDRACEAE), A MID-TERTIARY FOSSIL FLOWER IN DOMINICAN AMBER

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ABSTRACT

Ticodendron palaios is described as a new species of fossil flower preserved in amber from Mid-Tertiary deposits in the Dominican Republic. The genus, newly described in 1989 (Gómez-Laurito & Gómez-P. 1989), is arborescent and limited to regions of wet primary forests in Central America, ranging from southern Mexico to Panama. It was made a separate family, Ticodendraceae, by Gómez-Laurito and Gómez-P. (1991) and assigned to the hamamelidalian order Fagales. The fossil species is represented by a single pistillate flower and consists of a partial inflorescence with 1 short-pedicelled, inferior ovary subtended by 4 large bracts and surmounted by 3 short sepals and 2 papillate styles. The sepals, ovary, and pedicel are densely hispid-setose. The flower shows an overall resemblance to the original species, *T. incognitum*, with some important differences, one being that its styles, instead of being extended, are appressed to the ovary. However, this could be due to the flower's position at the edge of the resin exudate before it was fossilized.

RESUMEN

Se describe **Ticodendron palaios** como una nueva especie fósil de flor preservada en ámbar en depósitos del Terciario medio en la República Dominicana. El género, descrito en 1989 (Gómez-Laurito & Gómez-P. 1989), es arborescente y limitado a las regiones de bosques primarios húmedos en América Central, que van del sur de México a Panamá. Se hizo una nueva familia, Ticodendraceae, por Gómez-Laurito y Gómez-P. (1991) y se assignó al orden Fagales de las hamamelidas. La especie fósil está representada por una flor simple pistilada y consiste en una inflorescencia parcial con un ovario ínfero cortamente pedicelado, subtendido por 4 grandes brácteas y sobremontado por tres cortos sépalos y dos estilos 2 papilados. Los sépalos, ovario, y pedicelo son densamente híspido-setosos. La flor muestra un parecido general con la especie original, *T. incognitum*, con algunas diferencias importantes, una son sus estilos, que en vez de ser patentes, son apresados al ovario. Sin embargo, esto puede estar debido por la posición de la flor en el borde del exudado de resina antes de fosilizarse.

INTRODUCTION

Dominican amber is obtained from mines in the mountains of central Hispaniola and contains fossilized plant materials and animals, especially insects, which make it sought after by collectors. The marine strata containing the amber have been placed in the Mid-Tertiary period, but the exact dating is uncertain, due to two different published estimates derived from fossil organisms in the deposits. An age of 20–15 Ma was proposed (Iturralde-Vinent & MacPhee 1996) based on foraminifera, while studies of coccoliths yielded an estimate of 45–30 Ma (Cépek in Schlee 1999). The strata are composed of turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994).

The resin giving rise to the amber was produced by a leguminous tree, *Hymenaea protera* (Poinar 1991), a relative of the present-day Neotropical species *H. courbaril* L. The suite of amber-embedded organisms is representative of a moist tropical forest, which was described by Poinar and Poinar (1999) based on the known insect fauna together with whatever plant fossils were then available. The present flower is the 17th angiosperm species to be described from Dominican amber. Others are 1 species of Fabaceae (Poinar 1991), 3 of Arecaceae (Poinar 2002a, 2002b), 2 of Poaceae (Poinar & Judziewicz 2005, Poinar & Columbus 2012), 1 of Chrysobalanaceae (Poinar et al. 2008a, revised by Chambers & Poinar 2010), 2 of Lauraceae (Chambers et al. 2011a, 2012), 3 of Meliaceae (Chambers et al. 2011b, Chambers & Poinar 2012), 1 of Burseraceae (Chambers & Poinar 2013), 1 of Myristaceae (Poinar & Steeves 2013), 1 of Rhamnaceae (Chambers & Poinar 2014), and 1 possibly of Moraceae (Poinar et al. 2008b).

Our proposal to place the fossil in *Ticodendron* came from its similarity to illustrations and descriptions of *T. incognitum* published in Kubitzki (1993), and this relationship was later confirmed by examination of herbarium specimens. *Ticodendron* which was formally described only recently (Gómez-Laurito & Gómez-P. op. cit.) is a dioecious, arborescent, monotypic genus occurring in moist tropical forests of Central America, from southern Mexico to Panama. It had been collected infrequently in the past and was most often mistaken for *Alnus*, due to a similarity in leaf architecture (Hickey & Taylor 1991). The small, unisexual flowers were not well understood by earlier taxonomists, who were unable to place them in a known genus. Discovery of a fossil species of *Ticodendron*, if correctly assigned,, will help in understanding the history of the family and of the Tertiary Laurasian forests of which it is characteristic (Hammel & Burger 1991). These relationships are discussed in a later section.

MATERIALS AND METHODS

The fossil is contained in a rectangular block of amber measuring 8 × 4 × 4 mm. It was obtained from mines in the Cordillera Septentrional, between Puerto Plata and Santiago, Dominican Republic. Examination and photographs were made with a Nikon stereoscopic microscope SMA-10-R at 80× and a Nikon Optiphot microscope at 800×.

DESCRIPTION

Ticodendron palaios K.L. Chambers & Poinar, sp. nov. (**Figs. 1–2**). TYPE: HISPANIOLA. DOMINICAN REPUBLIC: amber mine in the northern mountain range (Cordillera Septentrional), 2013, *unknown amber miner s.n.* (HOLOTYPE: catalogue number Sd-9-192, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower single, pistillate, in a peduncled partial inflorescence (Tobe 1991), peduncle 1.9 mm long, lightly hispid, arising from a terminal or axillary bud with numerous, spirally arranged bud scales (Fig. 1), bracts subtending inflorescence 4, separate, lanceolate, acute, up to 1.9 mm long, 0.6 mm wide, glabrous (Figs. 1, 2), axillary scales, if any, not visible, ovary inferior, oblong-cylindric, 2.8 mm long, 1.5 mm wide, densely hispid-setose (Figs. 1, 2), pedicelled, pedicel 0.8 mm long, hispid-setose (Fig. 2), sepals 3 (2 visible), 0.7 mm long, 0.4 mm wide, oblong-lanceolate, obtuse, hispid-setose abaxially (Fig. 2), petals 0, styles 2 (?), densely papillate (Fig. 2), probably stigmatic throughout, unnaturally appressed to apex of ovary due to position of flower in the block of amber; staminate inflorescence unknown.

Etymology.—From Greek "palaios," ancient.

DISCUSSION

The apex of the flower is pressed against the edge of the block of amber (see Fig. 2), and there are an air bubble and granular artifact on one side (Fig. 1) that make interpretation of the styles and perianth difficult. Two sepals are evident in the other lateral view (Fig. 2), and the base of one folded-over style can be seen between them, bending sideways across the flower apex (Fig. 2). The styles otherwise can't be observed or measured. Air bubbles are present among the bracts (Figs. 1, 2), but these do not interfere with an interpretation of the inflorescence.

There are a number of significant differences between *Ticodendron palaios* and the extant species, *T. incognitum*. In the latter taxon, the inflorescence does not arise directly from a basal bud. Instead, it is terminal on a short lateral branch at whose tip is a pair of bracteate leaves (Gómez-Laurito & Gómez-P. 1989, Fig. 6F). Also, the two lower bracts subtending the flower are connate basally and a third bract is separate and displaced upward (pers. observ.); all 3 are densely strigillose-pubescent abaxially and glabrous adaxially (pers. observ.). In the fossil species, the bracts are 4, distinct throughout, and glabrous on both sides. The flower of *T. incognitum* is sessile, whereas in *T. palaios* it is borne on a short pedicel. The pubescence of the ovary in the extant species is lightly appressed-pilose, but in the fossil, it is densely hispid-setose. The sepals in *T. incognitum* are abundantly pilose-hispid adaxially, and these trichomes persist around the base of the styles in the developing fruit (pers. observ.). No such pubescence is seen in *T. palaios*. Leaf morphology, as well as the nature of the staminate inflorescence, is unknown in *T. palaios*, so that further comparisons with *T. incognitum* are not possible at present.

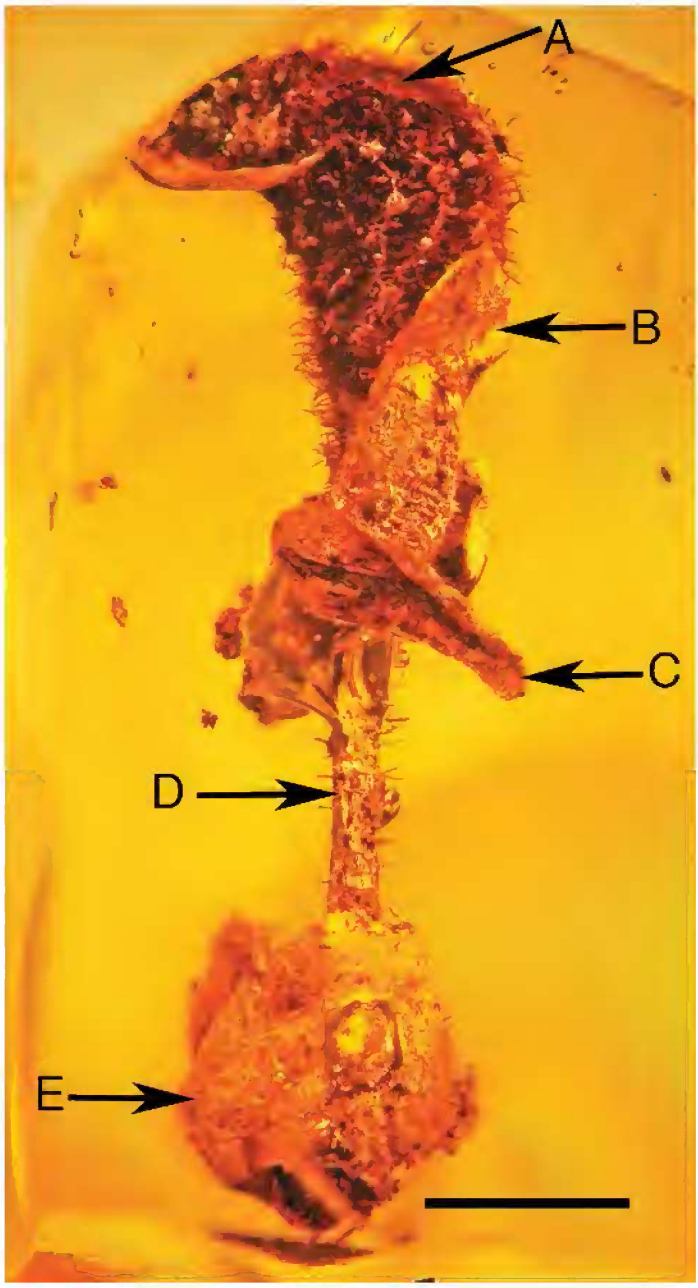

Fig. 1. ***Ticodendron palaios.*** **A: Terminal portion of one style lying over top of ovary. B and C: 2 of the 4 bracts subtending the flower. D: Peduncle of the inflorescence. E: Scale of the basal bud. The air bubble and granular material at upper left are artifacts. Scale bar = 1.3 mm.**

The anatomy, morphology, and relationships of *Ticodendron* were the subject of a series of papers published shortly after the genus was first described (Behnke 1991; Carlquist 1991; Feuer 1991; Hammel & Burger 1991; Hickey & Taylor 1991; Tobe 1991). The species had been collected a number of times in Central America, but it was not recognized as a unique genus until its alder-like leaves were brought together with its incon-

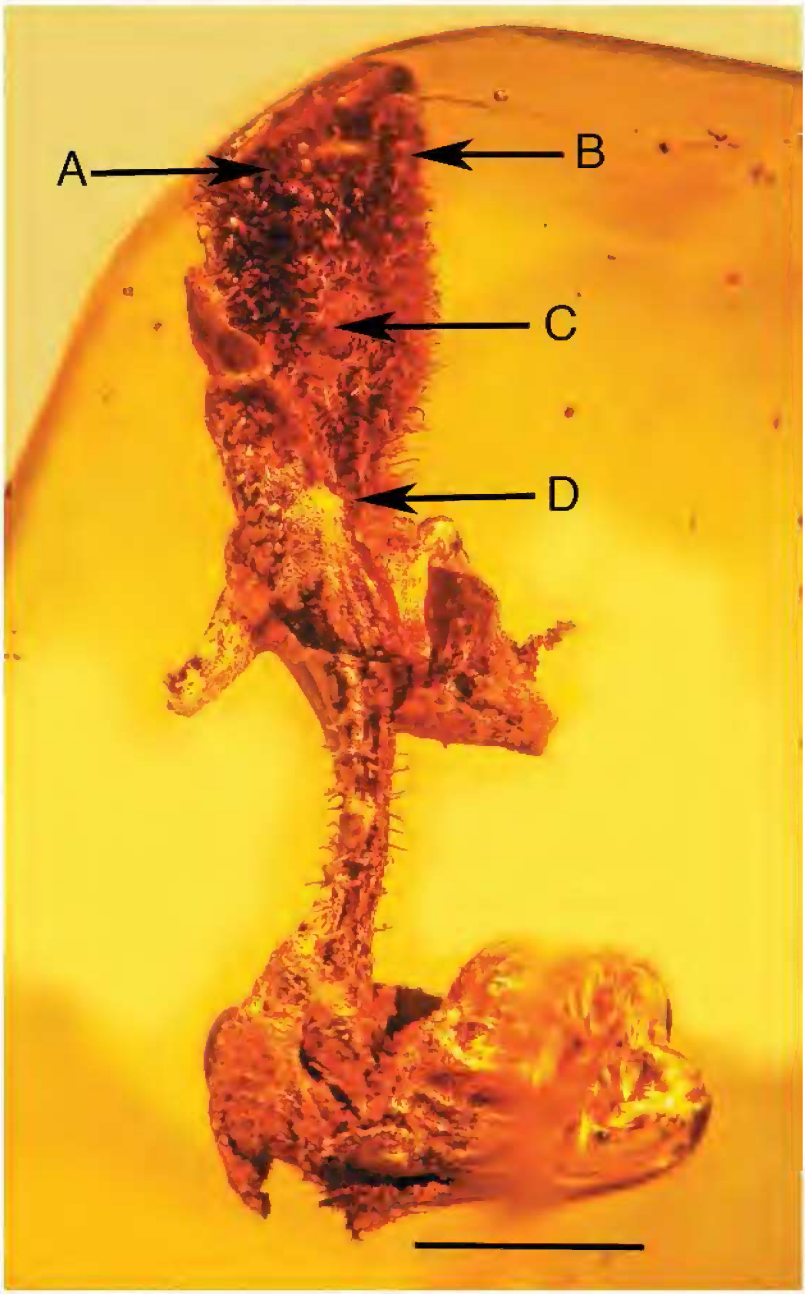

Fig. 2. *Ticodendron palaios*. Reverse lateral view of inflorescence. **A:** base of style. **B:** 1 of 2 visible sepals. **C:** ovary. **D:** floral pedicel. Scale bar = 1.5 mm.

spicuous male and female inflorescences by Gómez-Laurito and Gómez-P. (1989). The authors writing in 1991, above, considered several possible taxonomic orders in which to place the genus, including Juglandales, Myricales, Fagales, and Urticales. The totality of its wood and bark anatomy, pollen morphology, phloem sieve-elements, leaf architecture, and floral morphology led to its being classified as a monotypic family in order Fagales (Gómez-Laurito & Gómez-P. 1991).

Ecological relationships of the modern species, *Ticodendron incognitum,* were given special attention by Hammel and Burger (1991), who noted its occurrence in diverse, moist, evergreen cloud forests of middle-elevations, found on both sides of the continental divide throughout Mesoamerica. According to these authors, the fossil history of associated taxa indicates that they are members of a once widespread northern (Laurasian) forest flora of the Tertiary Period (Hammel & Zamora 1990). Studies of the leaf architecture of *T. incognitum* by Hickey and Taylor (1991) suggested a relationship with an Oligocene fossil taxon from Colorado, the genus *Fagopsis* (Manchester & Crane 1983). This relationship was confirmed in cladistic analyses of 48 principally vegetative characteristics (Hickey & Taylor, op. cit., Figs. 19–22). Even more convincing is its relationship to the Middle Eocene fossil fruit *Ferrignocarpus bivalvis* from the Clarno Formation in Oregon, assigned to Ticodendraceae by Manchester (2011). In this paper, Manchester also described identical fruits from the Early Eocene London Clay flora in England, which had been informally named "*Carpolithus* sp. 38" by Reid and Chandler (1933). In his discussion, Manchester (op. cit.) noted that this bicontinental disjunction "implies that the genus spread across higher latitudes and via the North Atlantic land bridge during the Late Paleocene and/or Early Eocene, when climatic conditions were suitable for the establishment of thermophilic taxa farther north." This analysis parallels the observations by Hammel and Burger (1991) and Hammel and Zamora (1990), mentioned above, concerning the history of present-day forests occupied by *Ticodendron* in Central America. From our studies of Dominican amber fossils, cited earlier, the following genera can be added to this forest type, as represented in the Caribbean region of the late Oligocene or early Miocene: *Roystonea, Trithrinax, Palaeoraphe, Alarista, Pharus, Hymenaea, Licania, Trochanthera, Swietenia, Trichilia, Persea, Treptostemon, Virola, Protium, Distigouania,* and *Ticodendron.*

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